Contrasting plant adaptation strategies to latitude in the native and invasive range of *Spartina alterniflora*

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Summary

- Biological invasions offer model systems of contemporary evolution. We examined trait differences and evolution across geographic clines among continents of the intertidal grass *Spartina alterniflora* within its invasive and native ranges.
- We sampled vegetative and reproductive traits in the field at 20 sites over 20° latitude in China (invasive range) and 28 sites over 17° in the US (native range). We grew both Chinese and US plants in a glasshouse common garden for 3 yr.
- Chinese plants were *c*. 15% taller, *c*. 10% denser, and set up to four times more seed than US plants in both the field and common garden. The common garden experiments showed a striking genetic cline of seven-fold greater seed set at higher latitudes in the introduced but not the native range. By contrast, there was a slight genetic cline in some vegetative traits in the native but not the introduced range.
- Our results are consistent with others showing that introduced plants can evolve rapidly in the new range. *S. alterniflora* has evolved different trait clines in the native and introduced ranges, showing the importance of phenotypic plasticity and genetic control of change during the invasion process.

Introduction

Biological invasions are a significant element of global change of the Anthropocene (Moran & Alexander, 2014; Kueffer, 2017), and provide opportunities to study contemporary evolution (Colautti & Lau, 2015). Most invasive species have occupied large geographic areas (Luque *et al.*, 2014; Seebens *et al.*, 2017) in which two distinct selection pressures might drive contemporary evolution between ranges or across latitudinal gradients. First, liberation of exotic plants from their natural enemies might lead to the evolution of increased vegetative and reproductive traits or novel latitudinal clines (Blossey & Nötzold, 1995; Bossdorf *et al.*, 2005). Second, geographic gradients in abiotic conditions might lead to the evolution of altered vegetative and reproductive traits or novel latitudinal clines (Bossdorf *et al.*, 2005; Colautti *et al.*, 2009; Colautti & Lau, 2015; Hodgins *et al.*, 2018). An important invasive mechanism is phenotypic plasticity, which allows the form and function of an organism to match the environmental variation encountered in a new environment without genetic modification (Richards *et al.*, 2006; Davidson *et al.*, 2011; Castillo *et al.*, 2018). Preadaptation is another mechanism facilitating invasion by which there is an incidental match of a genetically distinct subset of phenotypes to the particular introduced environments (Maron *et al.*, 2004; Dlugosch & Parker, 2007). Moreover, rapid evolution can also enable the establishment and spread of invasive species in the face of new selective pressures (Huey *et al.*, 2000; Maron *et al.*, 2004; Colautti & Barrett, 2013; Turner *et al.*, 2014; Oduor *et al.*, 2016; van Boheemen *et al.*, 2019). Parsing the relative influence of these multifarious mechanisms is the route to understanding contemporary evolution and adaptation in invasions (Colautti & Barrett, 2013; Colautti & Lau, 2015).

Studies of latitudinal clines within native and introduced ranges can provide considerable insight into rapid evolution of species invading new continents (van Kleunen *et al.*, 2018). Some biogeographic studies of introduced and native plants have explored how selection on traits varies across latitude (Maron *et al.*, 2004; Colautti *et al.*, 2009), with most studies finding that traits of native and exotic species evolve in parallel (Dlugosch & Parker, 2008; Etterson *et al.*, 2008; van Kleunen & Fischer, 2008; van Boheemen *et al.*, 2019; Latimer *et al.*, 2019). Some studies, by contrast, have found that the same traits of a single species have developed different latitudinal clines in the native and invasive ranges (Alexander *et al.*, 2012), and we lack a general understanding of why parallel clines sometimes develop and sometimes not, and of how the relative importance of phenotypic plasticity and genetic control of these clines changes during the invasion process.

Reproductive traits may change during geographic spread and invasions, and influence the rate and pattern of evolutionary process (Hairston *et al.*, 2005; Barrett *et al.*, 2008). Recent research has found that fecundity plays a critical role in the spread of introduced species, especially under variable environmental conditions (Hayes & Barry, 2007; Pyšek & Richardson, 2007; Simberloff, 2009; van Kleunen *et al.*, 2010). Fecundity is driven in part by plant size, which determines the availability of resources for sexual reproduction (Klinkhamer *et al.*, 1997; Liu & Pennings, 2019). Plant size will also affect competitive interactions with native species and conspecifics, because taller plants are better competitors for light (Keddy, 2001). Therefore, whether reproductive and vegetative traits evolve different latitudinal clines in the native and invasive ranges is likely to greatly affect both the spread of the invasive and interactions with native species.

Here, we consider *Spartina alterniflora* Loisel, a monoecious, wind pollinated, long-lived clonal plant of low-energy marine shores in North America, and its introduction to China. *S. alterniflora* spreads locally by clonal growth, and over longer distances by floating seeds (Daehler & Strong, 1994; Strong & Ayres, 2013). The native range of *S. alterniflora*, from Mexico in the Gulf of Mexico to Nova Scotia in North America, has a broad spectrum of abiotic conditions of temperature, growing degree day, precipitation, tide range, soil organic content, and soil water content (Pennings & Bertness, 2001; Strong & Ayres, 2013). Likewise, vegetative traits of *S. alterniflora*, such as stem height, diameter, density, leaf size, flowering time, and palatability to herbivores, are highly variable over the native range (Turner, 1976; Kirwan *et al.*, 2009; Travis & Grace, 2010; Crosby *et al.*, 2017), with a genetic basis for some variation shown by persistence in common garden experiments in the native range (Seliskar *et al.*, 2002; Crosby *et al.*, 2015). Molecular analyses show fine-scale spatial genetic structure in *S. alterniflora* (Hughes, 2014). Genetic structure varies across latitude in the native range, with cpDNA haplotypes and Bayesian analysis of microsatellites distinguishing locations south of Virginia from more northerly sites (Blum *et al.*, 2007; Qiao *et al.*, 2019).

Since its introduction into China in 1979, *S. alterniflora* has spread widely by natural dispersal and deliberate planting from a midlatitude site in Luoyuan in Fujian, China in 1980 (Xu & Zhuo, 1985). To date, it has spread southward to Hainan Island (19.70°N) and northward well into North Korea (39.90°N) (Liu *et al.*, 2016). This invasion is the largest and most recent of many substantial invasions of *S. alterniflora* around the world (Strong & Ayres, 2013). *S. alterniflora* is preadapted to the habitat of this invasion; abiotic and biotic conditions in China are similar to those on the Western North Atlantic shores where *S. alterniflora* evolved (Kirwan *et al.*, 2009; Crosby *et al.*, 2015; Liu *et al.*, 2016). The spread in China is into a virtually empty niche: no native vascular plant occupies most of this habitat in China, and *S. alterniflora* has been, by and large, released from interspecific competition (Li *et al.*, 2009; Cui *et al.*, 2016).

Populations of *S. alterniflora* in China are more productive than the native populations in North America (Qing *et al.*, 2012; Shang *et al.*, 2015), but geographic variation in standing biomass appears to be driven by the same abiotic factors in the native versus introduced range (Liu *et al.*, 2019). It is unclear to what extent the greater productivity in the introduced range is due to the specific source sites of the invasion (i.e. founder effects), phenotypic plasticity or evolution in China. Moreover, previous work has identified genetic by environment interactions that showed the evolution of reproductive traits in the introduced range (Liu *et al.*, 2017), but little information is known about geographic variation in reproductive traits in the native range, and so we cannot assess how selection on reproductive traits differs between the native and introduced ranges.

Here, we compared traits related to growth (plant height and shoot density) and sexual reproduction (seed set) between 20 populations in China and 28 populations in the USA, by sampling across latitude in the field and growing plants from the various populations in a glasshouse common garden. Building on previous results, we asked the following three questions: (1) Do vegetative and reproductive traits of *S. alterniflora* differ between the native and introduced ranges? (2) How is geographical variation in *S. alterniflora* vegetative and reproductive traits influenced by climatic variation within and between ranges? (3) Do latitudinal patterns in the introduced range parallel those in the native range? We hypothesised that: (1) populations of *S. alterniflora* from the introduced range would out-perform native populations; (2) geographical variation in *S. alterniflora* traits would be driven by the same variables in the native and introduced ranges; and (3) trait variation in introduced populations would parallel latitudinal patterns in the native range.

Materials and Methods

Study sites and species

To study the performance of *S. alterniflora* in the introduced and native ranges, we sampled plants across a wide latitudinal gradient in China (introduced range) and in North America (native range). All invasive *S. alterniflora* populations in China have spread from introductions in 1979 at Luo Yuan Bay, Fujian Province, 26.50°N (LY, Fig. 1a) that originated from three sources in the USA: Morehead City, North Carolina (34.72°N), Sapelo Island, Georgia (31.47°N), and Tampa Bay, Florida (27.70°N) (Xu & Zhuo, 1985; Guo *et al.*, 2015; Bernik *et al.*, 2016). We refer to these as 'source' populations, and other populations in the USA as 'nonsource' populations. In China we sampled 10 locations ranging from 20.90°N to 39.05°N (Fig. 1a) in September–November, 2014 (Supporting Information Table S1). To standardise phenology, we started at the southernmost location (Leizhou) when seed set began in late September and ended at the northernmost location (Tanggu) when seeds were being set in early November (in China, *S. alterniflora* flowers earlier at low vs high latitudes, X. C. Chen *et al.*, unpublished). In the USA, we sampled 14 locations ranging from 27.70°N to 43.32°N (Fig. 1b) in October and November 2014 (Table S1). Within each location, we worked at two sites, 2–3 km apart, with 20 sites in China, and 28 sites in the USA. In both geographic ranges, *S. alterniflora* occupies lower elevations in the intertidal than other plant species. In China, higher elevations

may be occupied by mangroves at low latitudes and *Phragmites australis*, *Scirpus mariqueter* and *Suaeda salsa* at higher latitudes (Li *et al.*, 2009, 2014; Cui *et al.*, 2016). In the USA, higher elevations are commonly occupied by *Juncus roemerianus* at low latitudes and *Juncus gerardii* and *Spartina patens* at higher latitudes (Pennings & Bertness, 2001).

Almost all salt marsh plants vary in phenotype across elevational gradients (Richards *et al.*, 2005). *S. alterniflora*, in particular, is well known to vary in morphology with marsh elevation (Pennings & Bertness, 2001); therefore, elevation in the marsh had to be standardised in order to make meaningful geographic comparisons. Many high marshes in China are intensively reclaimed for agriculture, aquaculture and industrial development (Li *et al.*, 2009; Cui *et al.*, 2016), and so it would be difficult to sample 'short-form' *S. alterniflora* at intermediate marsh elevations in China. As a practical matter, the easiest way to standardise elevation across all sites was to focus on the tall form *S. alterniflora*, which we defined as the tallest plants that were growing at each site. These plants were invariably growing low in the marsh or along creek banks, and always occurred in monospecific stands. At each site, we sampled five 0.5 × 0.5 m quadrats in tall form *S. alterniflora* stands, with individual quadrats spaced >30 m apart.

Traits

A key vegetative trait of *S. alterniflora* is plant height (Hughes, 2014), because it correlates highly with a suite of other variables related to vegetative growth. In each quadrat, we measured the height of the three tallest *S. alterniflora* shoots and counted the number of shoots that were >25 cm tall (= shoot density). *S. alterniflora* stands often have large numbers of very short shoots, but these do not contribute importantly to standing biomass (Morris & Haskin, 1990). We randomly collected 10 inflorescences within a metre of each quadrat. For samples from the USA, we counted the number of filled seeds in each inflorescence, distinguishing filled from unfilled seeds (Daehler & Strong, 1994; Liu *et al.*, 2016). Filled seeds have an embryo, endosperm, and can potentially germinate and grow; unfilled seeds have neither of these tissues and cannot germinate or grow (Daehler & Strong, 1994; Ayres *et al.*, 2008). We previously documented latitudinal trends in seed sets at the same sites in China in 2012 and 2013 (Liu *et al.*, 2016), therefore we made seed collections in China in 2014 but did not repeat estimates of seed sets. To compare seed sets between the USA and China, we used data from China for 2013 (Liu *et al.*, 2016). We calculated both seed set (100 × filled seeds/total seeds) and seed production (number of flowering stems × number of filled seeds). Because the two measures showed the same pattern (Liu *et al.*, 2016), we only choose the seed set as the indicator of sexual reproduction. Year-to-year variation affects plant growth and sexual reproduction (Liu & Pennings, 2019), but this variation is weaker than latitudinal patterns (Liu *et al.*, 2016).

Environmental variables

To relate the performance of *S. alterniflora* to abiotic conditions, we calculated annual average daily temperature, the annual

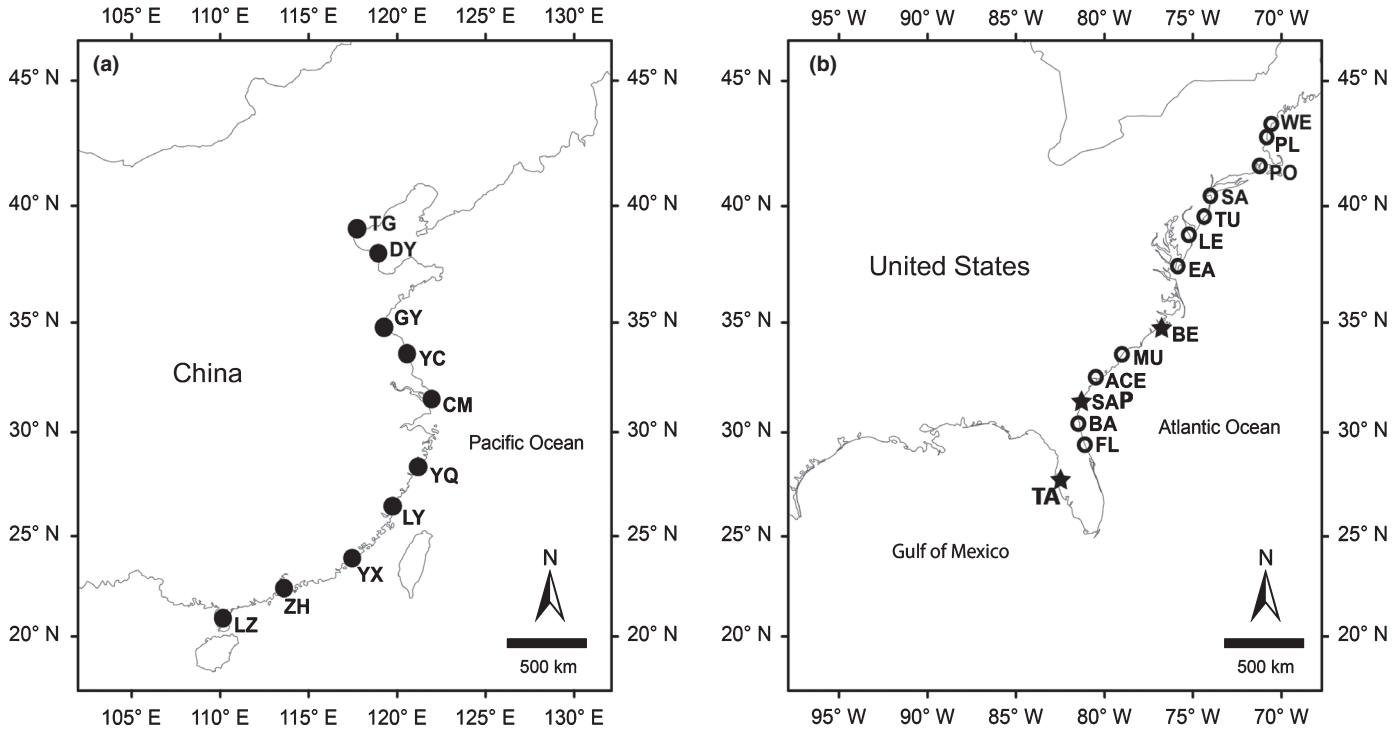

Fig. 1 Map of *Spartina alterniflora* survey locations in the: (a) introduced (closed circles), and (b) native (open circles) ranges. Three source sites are indicated with asterisks. Site details are found in Supporting Information Table S1.

number of growing degree days (>10°C) (Kirwan *et al.*, 2009), annual precipitation, and annual mean tide range for each location using climate data (1981–2010) and tide range (2013–2015) from NOAA (NCDC, http://www.ncdc.noaa.gov) for sites in the USA. Growing degree days was dropped from the analysis because it was highly correlated with average daily temperature ($R^2 = 0.99$). Parallel climate and tide range data for China were obtained from the China Meteorological Data Service Center (CMDC, http://data.cma.cn), and tide tables published by the National Marine Data and Information Service (NMDIS, http://www.nmdis.gov.cn). We also measured porewater salinity (PSU) at each location using the soil rehydration method (Pennings & Richards, 1998), but because we were working in the low intertidal which was daily flooded by the tides, it did not vary with latitude in either range (data not shown).

Common garden

To determine if differences in performance of *S. alterniflora* between the introduced and native ranges were due to genetic differences or differences in abiotic conditions, we conducted a common garden experiment in a glasshouse at the Xiang'an campus of Xiamen University (24.62°N, 118.31°E). Although this glasshouse was in the lower-latitude part of the range of *S. alterniflora*, previous work has found broadly similar patterns of growth and reproduction for Chinese plants grown in three common gardens that spanned most of the latitudinal range (Liu *et al.*, 2017). The glasshouse had a plastic roof to exclude rain and mesh sides to exclude insects. The common garden consisted of 10 rectangular plastic pools (length: 1.2 m, width: 0.9 m, depth: 0.3 m). Each plastic pool contained 24 plastic buckets (18 cm in diameter and 24 cm deep), which were grouped into four rows and six columns. Each bucket was filled with a mixture of 50% Jiffy's peat substrate (Jiffy Products International BV, Moerdijk, the Netherlands) and 50% vermiculite (v/v), and had four 1 cm diameter holes in the sides and one in the bottom to allow exchange of water with the water in the pool. Pools were filled with artificial sea water (10 PSU) to *c.* 2 cm above the soil level in the pots. Salinity was checked every other day and fresh water was added as needed to maintain salinity. These conditions were within the range experienced by plants in the field, and were chosen to minimise abiotic variation within and among pots. Water in the pools was completely replaced once a month. Fertiliser (C : N : P, 15 : 15 : 15; 0.5 g per plant) was added to the pools in March 2015.

In March 2015, seeds from each quadrat were germinated and grown in a growth chamber until seedlings were *c.* 5 cm tall. One randomly chosen seedling per quadrat (100 from China; 140 from the USA) was transplanted into a single, randomly selected plastic bucket, with each location (10 from China; 14 from the USA) replicated once in each of the 10 pools.

Using protocols developed in our earlier study (Liu *et al.*, 2016, 2017), in October 2015 we measured the height of the three tallest shoots in each pot when most of plants had reached maturity in pots. If fewer than three shoots were present, we measured all the shoots. We then counted the number of shoots that were >25 cm tall in each bucket. We collected inflorescences from the tallest three flowering stems, and counted the number of filled seeds. If fewer than three flowering shoots were present, we sampled all the shoots. In March 2016, we separated a 15–20 cm long rhizome bearing one or two shoots from each clone, transplanted the rhizome into a new bucket in a new soil mixture, and fertilised the pool as above. This process was repeated in 2016–2017, to give 3 yr of data. Thus, data from each of the 3 yr in the common garden were obtained from the same clones that were propagated by rhizomes from 1 yr to the next.

Statistical analyses

For statistical analyses, field and common garden data for the five seed families from each site were averaged to yield a single data point for each site (i.e., two data points per location). We used two-sample *t*-tests to test for differences in plant height, shoot density and seed set between the introduced and native ranges, and between source and nonsource populations in the USA in the field and common garden. Data were log(x)-transformed or square-root(x)-transformed or arcsine (sqrt(x))-transformed to improve the normality of errors and homogeneity of variance when necessary. We analysed each year of data from the common garden separately because we were primarily interested in differences between the two ranges rather than temporal changes. Because the same clones were analysed in the 3 yr of the common garden and plant height, shoot density and seed set changed in mean scores over 3 yr, we used repeated measures analysis of variance (ANOVA) to compare plant height, shoot density and seed set between the introduced and native ranges to develop a time course for region effect. We used linear and quadratic regression to analyse the relationships between plant traits (height, shoot density and seed set) and latitude of origin in the field and common garden. To confirm the effects of source type (source vs nonsource) in the native range across years, we used a mixed model with source type, year, and source type × year as fixed factors, and with subsite families nested in location and block as random effects. To confirm the effects of latitude by range across years, we used a mixed model with latitude, year, and latitude × year as fixed factors, and with subsite families nested in location and block as random effects. To confirm the differences of latitudinal clines between ranges, we compared between ranges using mixed models with range, latitude, range × latitude, and range × latitude^2 as fixed factors, and with subsite families nested in location and block as random effects.

To determine the relative influence of the different abiotic factors on plant traits, we used linear and quadratic regression to analyse the relationships between plant traits in the field and abiotic variables (annual mean temperature, precipitation and tide range); we pooled the data from both geographic regions and used multiple regression to generate single relationships to predict each plant trait. For each trait, we examined a full model consisting of region, temperature (or temperature^2 for nonlinear relationships), precipitation, tide range, region × temperature (or temperature^2 for nonlinear relationships), region × precipitation, and region × tide range to detect the most important factors. Best regressions were selected using stepwise regression based on the Akaike information

criterion (AIC). We performed all analyses using R statistical software (R Development Core Team, 2019); see Notes S1.

Data availability

All data for this publication were deposited in the Georgia Coastal Ecosystems Long Term Ecological Research repository at https://gce-lter.marsci.uga.edu/public/app/dataset_details.asp?accession=BOT-GCED-1912 (Pennings, 2019, Contrasting plant adaptation strategies to latitude in the native and invasive range of *Spartina alterniflora*: geographic survey (2014) and common garden (2015–2017). Georgia Coastal Ecosystems LTER Project, University of Georgia, Long Term Ecological Research Network, http://dx.doi.org/10.6073/pasta/b83b995ed23d9224f8846aa1d7e4b59d).

Results

In both the field survey and the common garden experiment, plants from the introduced range generally outperformed plants from the native range (Fig. 2; Table 1). The key reproductive trait of seed set was more than two times greater in the field (Fig. 2i) and up to four times greater in the common garden (Fig. 2j) in the introduced versus the native range. In the field survey, the invasives were on average 20% taller and 17% denser than native plants (Fig. 2a,e), while in the common garden these two vegetative traits were 20–40% and 15–30% greater, respectively, in the invasives versus the natives (Fig. 2b–d,f–h).

Repeated measures analysis

For the common garden, with years considered in the aggregate using repeated measures ANOVA, the Chinese populations were greater in both vegetative and reproductive traits (Fig. S1). Chinese plants were taller ($F_{1,132} = 39.50$, $P < 0.0001$), but height did not differ among years ($F_{1,132} = 2.26$, $P = 0.135$) or in the interaction between region and years ($F_{1,132} = 1.46$, $P = 0.229$). Likewise, Chinese plants were denser ($F_{1,132} = 29.81$, $P < 0.0001$) and density differed among years ($F_{1,132} = 17.24$, $P < 0.0001$), but there was no interaction between region and years ($F_{1,132} = 0.46$, $P = 0.501$). Seed set varied differently over time for plants from the two ranges (Region × Year: $F_{1,132} = 7.15$, $P = 0.0085$), with seed set higher for introduced versus native plants in the 1st year but declining to low levels for all plants by the 3rd year.

Source sites

The source sites from which the seeds were collected and that produced the introduced populations in China (Tampa Bay, TA; Sapelo Island, SAP; Beaufort North Carolina, BE), did not differ in height or shoot density from the nonsource, North American sites in either the field survey or in the common garden, except for shoot density in the 1st year of the common garden (Fig. 2a–h; Table S2). Field seed set in the source sites was actually *c.* 50% lower than seed set in the nonsource sites, but this difference disappeared in the common garden (Fig. 2i–l).

Latitude and traits

In the field, both introduced and native populations exhibited strong latitudinal clines in plant height, shoot density and seed set. For height and shoot density, the field clines were respectively hump shaped (convex) (Fig. 3a; Table 1) and U shaped (concave) (Fig. 3e; Table 1). In the common garden, the hump-shaped pattern of height for introduced populations disappeared, but the hump-shaped pattern of height for the native populations persisted (Fig. 3b–d; Table S3). In the common garden, the U-shaped pattern of shoot density disappeared for both introduced and native populations (Fig. 3f–h; Table S3). For seed set in the field, the introduced populations showed a distinct linear increase with the highest latitudes producing an average of *c.* 78% filled seeds, which was over five times greater than the seed set of the lowest latitude populations, which had an average of *c.* 14% filled seeds. For the native populations in the field, seed set showed a convex pattern, which is different from invasive range (Table 1), with midlatitudes producing *c.* five-fold the seed of the lowest and highest latitudes (Fig. 3i). However, no latitudinal relationship of seed set was manifested in the common garden for the native populations. The latitudinal pattern of Chinese plants from high latitudes exhibiting a higher percentage of filled seeds and greater seed set persisted through the 3 yr in the common garden, although the magnitude of seed set declined each year (Fig. 3j–l; Table S3).

Environmental variables and traits

The relationships between plant traits and latitude observed in the field can also be expressed as relationships with abiotic variables. Plant height showed hump-shaped relationships with annual mean temperature in both the introduced and native ranges (Fig. S2a) that was unrelated to precipitation in either region (Fig. S2b) and showed a positive relationship to tide range in the introduced range but a hump-shaped relationship to tide range in the native range (Fig. S2c). Shoot density showed U-shaped relationships with annual mean temperature in both the introduced and native ranges (Fig. S2d), a hump-shaped relationship with precipitation in the introduced range (Fig. S2e) and a declining relationship with tide range in the introduced range (Fig. S2f). Seed set showed a declining relationship with annual mean temperature and precipitation in the introduced range (Fig. S2g–h) and a hump-shaped relationship with annual mean temperature in the native range (Fig. S2g). On average, seed set was *c.* 70% lower in the native range than in the introduced range (Fig. S2g). Therefore, individual abiotic variables were related to plant phenotypes differently in the two regions. A similar analysis for the common garden results indicated that the height of plants from the USA in the common garden was best predicted by temperature at the field sites (Fig. S3a–c), but that seed set of Chinese plants in the common garden was well predicted by temperature (Fig. S3g–i) or precipitation (Fig. S4g,i) at the field sites. No significant relationships were found between traits of native and invasive plants in the common garden and tide range at the field sites (Fig. S5).

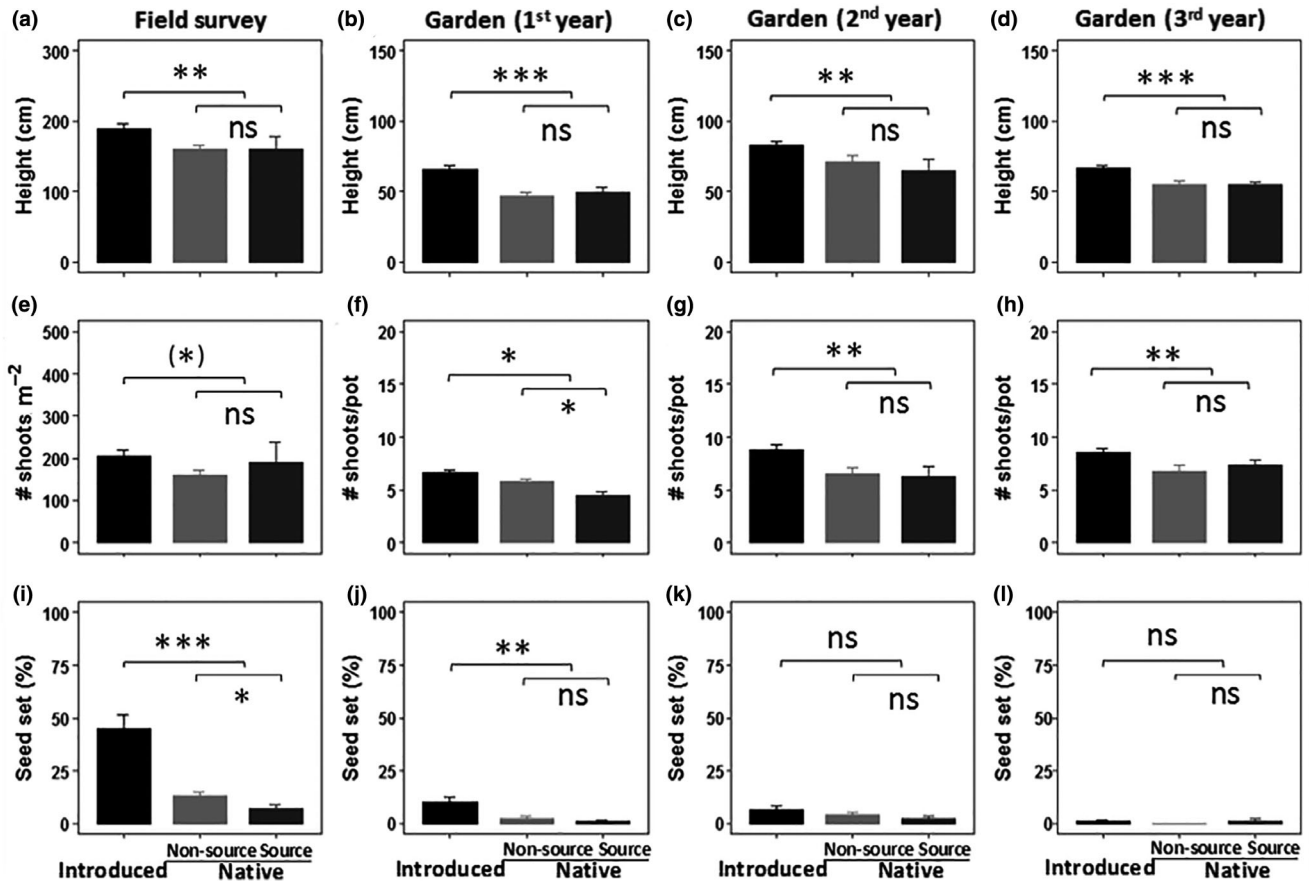

Fig. 2 Plant height (a–d), shoot density (e–h), and seed set (i–l) of *Spartina alterniflora* populations from introduced (China) and native (USA) ranges in the field (a, e, i) and over 3 yr in the common garden (b–d, f–h, j–l). Data are means + 1 SE. Asterisks indicate significance of *t*-tests between the introduced and native range, and between source and nonsource populations in the native range. ns, $P > 0.1$, (*) marginal, $P = 0.05$–0.06; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Modelling trait variation

To go beyond individual effects of the abiotic variables, we made a statistical model of their combined effects upon plant performance in the two regions. We used the predictor variables native or introduced region, temperature, precipitation and tide range to find the best linear and quadratic regression for these variables. Plant height was best predicted by temperature and the interaction between region and tide range, although other variables also were retained in the best regression (Table 2; Fig. 4a). Shoot

Table 1 Mixed model analysis of latitudinal clines and phenotypic differences between native and invasive populations of *Spartina alterniflora* in the field and 3-yr common garden, with subsite populations nested in location and block as random effect.

Growth condition	Trait	Range	Latitude	Latitude^2	Range × latitude
Field	Plant height (cm)	**$7.33_{1,\ 18}$***	**$13.62_{1,\ 18}$****	**$13.76_{1,\ 18}$****	$0.11_{1,\ 18}$$^{(ns)}$
	no. shoots/m^2	$1.47_{1,\ 18}$$^{(ns)}$	**$13.91_{1,\ 18}$****	**$14.63_{1,\ 18}$****	$2.20_{1,\ 18}$$^{(ns)}$
	Seed set (%)	**$97.69_{1,\ 20.02}$*****	**$38.77_{1,\ 19.99}$*****	–	**$20.84_{1,\ 19.99}$*****
Garden 1st year	Plant height (cm)	**$48.14_{1,\ 17.78}$*****	**$5.11_{1,\ 17.83}$***	**$4.65_{1,\ 17.91}$***	$0.19_{1}$$^{(ns)}$
	no. shoots/m^2	**$14.66_{1,\ 19.66}$****	**$11.05_{1,\ 20.13}$****	–	$0.02_{1,\ 20.19}$$^{(ns)}$
	Seed set (%)	**$29.79_{1,\ 19.60}$*****	**$19.12_{1,\ 20.14}$*****	–	**$14.42_{1,\ 20.23}$****
Garden 2nd year	Plant height (cm)	**$4.21_{1,\ 16.83}$***	$1.02_{1,\ 17.73}$$^{(ns)}$	–	**$4.73_{1,\ 21.66}$***
	no. shoots/m^2	**$11.52_{1,\ 16.93}$****	$2.05_{1,\ 17.62}$$^{(ns)}$	–	$2.37_{1,\ 22.59}$$^{(ns)}$
	Seed set (%)	**$3.85_{1,\ 16.61}$$^{\#}$**	$2.17_{1,\ 16.99}$$^{(ns)}$	–	**$7.38_{1,\ 23.23}$***
Garden 3rd year	Plant height (cm)	**$8.28_{1,\ 16.58}$***	$0.89_{1,\ 18.19}$$^{(ns)}$	–	**$9.31_{1,\ 19.83}$****
	no. shoots/m^2	**$4.58_{1,\ 16.75}$***	$0.08_{1,\ 18.26}$$^{(ns)}$	–	$2.61_{1,\ 19.62}$$^{(ns)}$
	Seed set (%)	**$3.54_{1,\ 16.30}$$^{\#}$**	**$4.54_{1,\ 18.28}$***	–	$2.41_{1,\ 20.31}$$^{(ns)}$

Entries in bold indicate statistically significantly results, significant level: ns, $P > 0.1$; #, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The quadratic latitude term was dropped from the model if not significant.

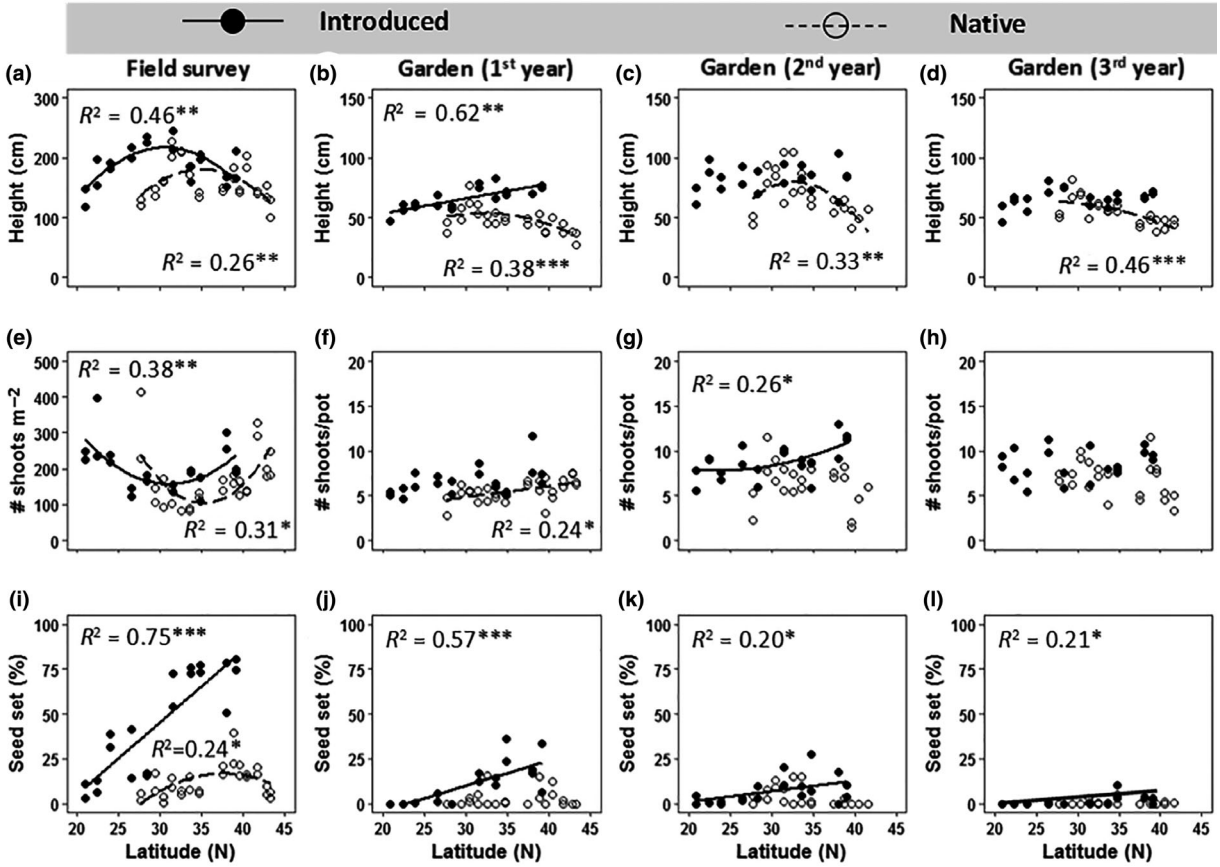

Fig. 3 Relationships between plant height (a–d), shoot density (e–h), and seed set (i–l) and latitude of origin in the field (a, e, i) and over 3 yr in the common garden (b–d, f–h, j–l). Trendlines are given only for significant relationships: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

density was best predicted by temperature and tide range (Table 2; Fig. 4b). Seed set was best predicted by region, temperature, and tide range (Table 2; Fig. 4c). Therefore, in all three cases, this analysis indicated that plant traits were partly a function of region, and not only driven by abiotic conditions.

Discussion

We found different genetic clines of native and invasive populations of *Spartina alterniflora* across latitude, with evidence for cline differentiation in vegetative growth among native populations that are likely to have been under selection for competitive ability (Travis & Grace, 2010), and strong evidence for cline differentiation in sexual reproduction in the invasive range under a vacant niche (Dlugosch *et al.*, 2015). The rapid clinal evolution of traits of *S. alterniflora* during the invasion of China provides a clear example of trait evolution during invasion. Rapid evolution of invasive species can determine invasion success (Hodgins *et al.*, 2018; van Kluenen *et al.*, 2018). In 38 yr, the invasive populations evolved a distinct cline, with high-latitude plants setting *c.* 78% filled seeds, over five times greater than that of low-latitude plants. This pattern persisted in the common garden, with high-latitude plants again setting several times more seed than low-latitude plants. This finding reinforced previous work (Liu *et al.*, 2016, 2017; Qiu *et al.*, 2018) and indicated the evolution of increased fitness in China (Hypothesis 1). The evolution of high fecundity may contribute to the rapid spread of *S. alterniflora* at high latitudes in China, consistent with the idea that fecundity plays a critical role in the spread of introduced species (Hayes & Barry, 2007; Pyšek & Richardson, 2007; Simberloff, 2009; van Kleunen *et al.*, 2010). No such cline existed in the native North American plants, which also had a considerably lower seed set of only up to 5% in the common garden.

Plants were larger and more fecund in the introduced range than in the native range in both the field and the glasshouse common garden (Figs 2, S1), consistent with previous studies of *S. alterniflora* (Qing *et al.*, 2012; Shang *et al.*, 2015) and many other introduced species (Leger & Rice, 2003; Bossdorf *et al.*, 2005; Hierro *et al.*, 2005; Colautti *et al.*, 2009; van Kleunen *et al.*, 2010, 2018; Hodgins *et al.*, 2018). Large size would contribute to higher competitive ability when mixed with native species (Hodgins *et al.*, 2018); clonality would contribute rapid spread in local sites (Liu *et al.*, 2006). We found no evidence for founder effects. Our results show that both source and nonsource trait values in North America were lower than those in China, reinforcing the inference of evolution of greater seed set of *S. alterniflora* among the invasive populations; the increased seed set in China was not due to peculiar trait values of the sources (assuming that trait values at source sites had not changed in the 40 yr since their introduction). The only two of the 12

Table 2 Best regression models for variation in *Spartina alterniflora* traits in the field, with data pooled across the invasive and native ranges.

Variable	Model	R^2	*P*-value
Height	−399.12* + 309.56 Region + 67.51 Temperature** − 1.99 (Temperature)^2** + 0.02 Precipitation + 5.37 Tide Range − 33.94 Region × Temperature + 1.06 Region × (Temperature)^2 − 0.08 Region × Precipitation + 27.48 Region × Tide Range***	0.70	< 0.0001
Shoot density	873.96*** − 52.80 Region − 74.20 Temperature*** + 2.18 (Temperature)^2*** − 22.60 Tide Range* − 28.80 Region × Tide Range	0.45	< 0.0001
Seed set	77.12*** − 62.30 Region*** + 5.01 Temperature − 0.26 (Temperature)^2** − 0.02 Precipitation − 4.32 Tide Range** + 0.07 Region × (Temperature)^2	0.85	< 0.0001

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

comparisons between source and nonsource populations with differences showed source trait values (no. shoots and seed set) to be less than nonsource values (Fig. 2f,i)–the opposite of founder effects causing the biologically pertinent differences of the invasive plants. The common garden experiments suggested that the greater seed set and vegetative traits in China were based upon evolutionary change (Figs 2j, S1c), because the differences persisted for 3 yr in the common garden. We inferred that the lower seed set in the glasshouse than found in the field in China in this study, and the lower glasshouse seed set in this study compared with seed set in field common gardens in our previous studies (Liu *et al.*, 2016, Fig. 2e; Liu *et al.*, 2017, Fig. S1c), were artefacts due to the low numbers of plants in the glasshouse and, therefore, the paucity of pollen for this self-incompatible, wind pollinated plant (Davis *et al.*, 2004).

That *S. alterniflora* has evolved rapidly in the 4 decades since its introduction to China is consistent with the rapid evolution of other introduced plants (Colautti & Barrett, 2013; Colautti & Lau, 2015). The evolution of increased competitive ability (EICA) hypothesis, in which introduced plants escape from their native enemies and can therefore divert resources from defence to growth, improving their competitive ability (Maron *et al.*, 2004; Bossdorf *et al.*, 2005), might in part apply to *S. alterniflora* in China. *S. alterniflora* is consumed by insects in its native range (Gratton & Denno, 2005), snails (Silliman *et al.*, 2005), and crabs (Holdredge *et al.*, 2009), whereas in China *S. alterniflora* generally lacks herbivores (Li *et al.*, 2009). Therefore, it is reasonable that plants in China could re-direct resources from antiherbivore defence to growth.

In addition, the introduction process may have increased the vigour of *S. alterniflora* plants. During the introduction, *S. alterniflora* plants from three US provenances were cultivated together and crossed (Qiao *et al.*, 2019), and the most vigorous lineages were propagated (Qing *et al.*, 2012; Shang *et al.*, 2015), so that the rapid evolution of *S. alterniflora* may have been facilitated by hybrid vigour and artificial selection. Intraspecific hybrid vigour is thought to have played a role in the spread of other invasive species (Boyer *et al.*, 2008; Roy *et al.*, 2015; Glotzbecker *et al.*, 2016).

In the field, clines in plant height and shoot density peaked at different latitudes in the two geographic regions (Fig. 3; Table 1). These clines had lower slopes in the common garden than in the field, suggesting that they were, in part, plastic responses to the environment. The latitudinal cline in plant height was positive in the Chinese populations in year 1 of the common garden, but disappeared after that. The native populations displayed a generally negative slope in plant height with latitude in all 3 yr in the common garden. In North America, latitudinal patterns in *S. alterniflora* traits often have a strong

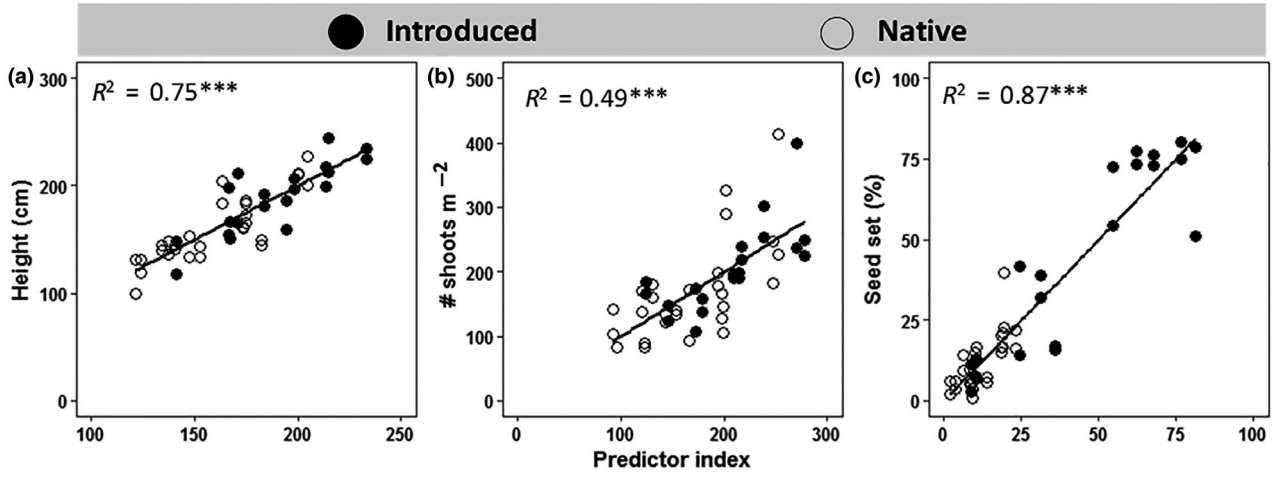

Fig. 4 *Spartina alterniflora* height (a), shoot density (b), and seed set (c) as predicted by the best regression model (Table 2). Significant levels for main effects: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

genetic component (Seliskar *et al.*, 2002; Travis & Grace, 2010). In our study, latitudinal clines in shoot density were less likely to reliably persist in the common garden, appearing in year 1 for the native populations, year 2 for the introduced populations, and absent in year 3 for both native and introduced plants.

In summary, most of the latitudinal variation in vegetative traits that was observed in the field disappeared in the common garden, except for plant height in the native range. Latitudinal variation in seed set in North American plants also disappeared in the common garden. Moreover, latitudinal variation in plant height and shoot density in both geographic regions could be explained by the same set of abiotic factors, indicating a common set of selective pressures in both regions on these traits. For Chinese populations, however, the linear increase in seed set with latitude in the field was preserved in the glasshouse, demonstrating rapid evolution of this reproductive trait in the introduced range.

Of all the traits, the latitudinal clines in seed set showed the greatest difference between the two geographic regions (Table 1), indicating different selective pressures across latitudes. When expressed as relationships with single abiotic variables in the field and common garden, seed set was again markedly greater in the Chinese populations, was strongly and negatively correlated with temperature and precipitation in China, but correlated weakly with temperature and not at all with precipitation in the native range (Figs S2g–i, S3g–i, S4g–i). In the regressions combining all abiotic variables, both vegetative traits and seed set were explained by a common set of predictor variables, but the best models included one or more highly significant terms containing 'region', indicating evolutionary differences between regions (Table 2). The resulting relationships had high R^2 values, indicating that the combination of evolutionary differences and the abiotic conditions that we examined was sufficient to explain a large proportion of the variation in *S. alterniflora* trait values across both geographic regions.

Our results were consistent with other studies that found temperature to increase *S. alterniflora* growth over most of its geographic range (Kirwan *et al.*, 2009; Idaszkin & Bortolus, 2011; Crosby *et al.*, 2017). However, at lower latitudes in the native range, high temperatures reduced *S. alterniflora* performance (Więski & Pennings, 2014), consistent with previous findings in China (Liu *et al.*, 2016, 2017; Qiu *et al.*, 2018). Because shoot density is negatively related to plant height (Liu & Pennings, 2019), shoot density was lowest when plants were tallest. Plant height increased with tide range, this result is consistent with the findings of Turner (1976) for *S. alterniflora* in its native range, and may be related to a decrease in sediment redox potential (Castillo *et al.*, 2005).

Propagule pressure is a major factor in the success of plant species establishing and invading a new habitat (Rouget & Richardson, 2003; Mason *et al.*, 2008; Li *et al.*, 2014). The greater seed set at high latitudes in China may be driven in part by increased flowering synchrony at high latitudes (Qiu *et al.*, 2018), and is associated with greater survival of seedlings (Liu *et al.*, 2017). High seed set is less beneficial in China at low latitudes, where seedling survival is lower due to high temperatures and high consumer pressure (Li *et al.*, 2014).

One caveat to our results is that we only sampled the tall form *S. alterniflora*. In the native range, *S. alterniflora* varies greatly in height, shoot density and flowering across elevation as a function of abiotic stress (Richards *et al.*, 2005; Liu & Pennings, 2019). *S. alterniflora* in China also retains similar plastic responses to elevation (Peng *et al.*, 2018; Zhu *et al.*, 2019). In the USA, sampling *S. alterniflora* in the 'midmarsh' produced similar latitudinal patterns as we have described here for samples collected from the low marsh (Kirwan *et al.*, 2009; Liu *et al.*, 2019), so we hypothesised that, if we had included midmarsh sampling in this paper, contrasts between the native and exotic ranges would have been similar to those that we documented in the low marsh. Testing this hypothesis is a matter for future studies.

Our results indicated that *S. alterniflora* had evolved rapidly since arriving in China, with Chinese plants taller, denser and setting more seeds than ones from the native range. Moreover, the introduced plants had evolved a latitudinal cline in sexual traits that is not seen in their native range. The introduced plants, however, had not evolved the latitudinal pattern in plant height that manifests in the native range. We speculate that the difference in sexual reproduction is due to the opportunity for rapid spread in the introduced range within mudflat habitats that were largely empty of other plants (Dlugosch *et al.*, 2015; Zhang *et al.*, 2017). By contrast, plants in the native range grew in dense stands of conspecifics, with little or no open mudflat habitat available (Travis & Hester, 2005; Travis & Grace, 2010; Zerebecki *et al.*, 2017). We hypothesised that, under these conditions, sexual reproduction is less favourable because there are few unoccupied areas to colonise. Instead, plants must compete vegetatively with conspecifics, circumstances that would select against sexual reproduction and for traits that increase competitive ability. Moreover, our results may also improve our understanding into how vacant niches across geographic range create opportunities for introduced species to evolve different strategies in other ecosystems (Dlugosch *et al.*, 2015). Our study, however, did not directly measure competitive ability or compare selection for sexual reproduction and competitive ability between the two ranges, and so further work would be needed to confirm these putative mechanisms.

Many other invasive species display parallel trait or genetic clines across latitude in their invasive and native ranges (Dlugosch & Parker, 2008; Etterson *et al.*, 2008; van Kleunen & Fischer, 2008; van Boheemen *et al.*, 2019; Latimer *et al.*, 2019). In some cases, these clines have shifted over time, likely to have been in response to climate change (Umina *et al.*, 2005). The novel finding of our paper is that clines for some traits, especially seed set, were different in the different regions, possibly reflecting different ecological conditions in the two ranges, and that the genetic control for clines in some traits was also different, possibly reflecting a lack of time for evolution to act (Lande, 2009).

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Author contributions

DRS, SCP and YZ conceived the ideas and designed the study; WL, YZ, XC and KM-D conducted the experiment; WL, YZ, XC and KM-D analysed the data; all authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Traits variation over 3 yr in the common garden.

Fig. S2 Relationships between field traits and climatic factors.

Fig. S3 Relationships between traits in the 3-yr common garden and temperature.

Fig. S4 Relationships between traits in the 3-yr common garden and precipitation.

Fig. S5 Relationships between traits in the 3-yr common garden and tide range.

Notes S1 R code for analyses reported in the Tables and Figs.

Table S1 Geographical locations, abiotic conditions and sampling dates for all sites in China (East Coast) and USA (Atlantic and Gulf Coasts).

Table S2 Mixed model testing the effect of source type and year on selected traits.

Table S3 Mixed model testing the effect of latitude and year on selected traits.

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